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Witteveen, N.H.; White, Cheryl; Sánchez-Martínez, B.A.; Philip, A.; Boyd, Femke; Gosling, W.D.; McMichael, C.

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ARTICLE

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Pre-contact and post-colonial ecological legacies shape Surinamese rainforests

Nina H. Witteveen[1] | **Cheryl White**[2] | **Barbara A. Sánchez-Martínez**[1] | **Annemarie Philip**[1] | **Femke Boyd**[1] | **Roemer Booij**[1] | **Reyan Christ**[1] | **Santosh Singh**[2] | **William D. Gosling**[1] | **Dolores R. Piperno**[3,4] | **Crystal N. H. McMichael**[1]

[1]Department of Ecosystem and Landscape Dynamics, Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, Amsterdam, Netherlands

[2]Department of History, Faculty of Humanities, Anton de Kom University, Paramaribo, Suriname

[3]Department of Anthropology, Smithsonian National Museum of Natural History, Washington, DC, USA

[4]Smithsonian Tropical Research Institute, Ancon, Panama

Correspondence
Nina H. Witteveen
Email: n.h.witteveen@uva.nl

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Abstract

Disturbances in tropical forests can have long-lasting ecological impacts, but their manifestations (ecological legacies) in modern forests are uncertain. Many Amazonian forests bear the mark of past soil modifications, species enrichments, and fire events, but the trajectories of ecological legacies from the pre-contact or post-colonial period remain relatively unexplored. We assessed the fire and vegetation history from 15 soil cores ranging from 0 to 10 km from a post-colonial Surinamese archaeological site. We show that (1) fires occurred from 96 BC to recent times and induced significant vegetation change, (2) persistent ecological legacies from pre-contact and post-colonial fire and deforestation practices were mainly within 1 km of the archaeological site, and (3) palm enrichment of *Attalea*, *Oenocarpus* and *Astrocaryum* occurred within 0, 1, and 8 km of the archaeological site, respectively. Our results challenge the notion of spatially extensive and persistent ecological legacies. Instead, our data indicate that the persistence and extent of ecological legacies are dependent on their timing, frequency, type, and intensity. Examining the mechanisms and manifestations of ecological legacies is crucial in assessing forest resilience and Indigenous and local land rights in the highly threatened Amazonian forests.

KEYWORDS
Amazonia, human–environment interactions, Maroon, palaeoecology, palm enrichment, phytoliths, pre-Columbian, Suriname

INTRODUCTION

The Amazonian rainforest is the most biodiverse region on Earth (Antonelli et al., 2018; Brooks et al., 2006) and has been shaped by environmental gradients, climatic changes, evolutionary history, and biotic interactions (Hoorn et al., 2010; Kristiansen et al., 2009; Mittelbach et al., 2007; Ter Steege et al., 2006; Wright, 2002). The

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drivers behind current biogeographical patterns, however, remain largely unresolved (Condit et al., 2002; Foster et al., 1986; Hubbell, 2013; Pos et al., 2019; Rull, 2011). An emerging hypothesis is that ecological legacies, defined as the impact of disturbance events on ecosystems and their persistence over time, have helped shape observed patterns of species diversity and relative abundances (Levis et al., 2017; McMichael, 2021).

People have lived in the Amazon rainforest for more than 10,000 years (Roosevelt, 1999). They relied on hunting and fishing, fire, forest management, and have practiced crop cultivation for at least the last 6000 years (Bush et al., 2016; Clement et al., 2010; Erickson, 2000; Heckenberger et al., 2003; Oliver, 2008; Versteeg, 2003). The locations of soil modifications and earthworks suggest that large and complex societies existed, primarily in seasonal forests and within 15 km of river floodplains (Arroyo-Kalin, 2010; Bush et al., 2015; Denevan, 1996; Woods & Glaser, 2004; Lehmann et al., 2007; Neves & Petersen, 2006; Peripato et al., 2023; Prümers et al., 2022; Watling et al., 2017). But there is less evidence of large-scale human activities in aseasonal *terra firme* forests (Heijink et al., 2020; McMichael et al., 2012; Piperno et al., 2017, 2019, 2021). Fire in Amazonian forests (today and in the past) is mainly associated with human activities as many forests are too wet for natural ignitions to spread (Bush et al., 2008; Cochrane, 2003; Cochrane & Schulze, 1998; Gosling et al., 2021; Malhi et al., 2014). Fire can cause severe and persistent ecological consequences (Åkesson et al., 2023; Barlow & Peres, 2008; Bodin et al., 2020; Bush et al., 2016; Maezumi et al., 2018; McMichael et al., 2022). Such ecological legacies from fire, or cultivation, plant domestication, and agroforestry primarily occur within a few kilometers of archaeological sites (Bodin et al., 2020; Maezumi et al., 2018, 2022). They have been reported, however, up to 5 km (Levis et al., 2018, 2020) and 20 km (Franco-Moraes et al., 2019; Levis et al., 2017) of archaeological sites. Direct species enrichment and depletion have also occurred for the last centuries to millennia (Balée, 1993; Clement, 1988; Clement et al., 2015; Thomas et al., 2015), and it is hypothesized that the high abundances of useful species near river margins are ecological legacies from yet undiscovered archaeological sites (Levis et al., 2017). The modification of plant abundances, however, is not always persistent as many useful plant species are short lived (Åkesson et al., 2021). Palms, one of the most useful and common plant groups in Amazonia have increased in abundance in recent millennia, but the role of humans remains unclear (Bush & McMichael, 2016; Clement et al., 2015; Heijink et al., 2020; Piperno et al., 2019).

During the post-colonial period (after European arrival to the Americas in AD 1492), land use in Amazonia intensified due to global trade, enslavement practices, population expansion and industrialization (Boomgaard, 1992; Weinstein, 1983). Colonization also brought disease that resulted in widespread mortality of Indigenous people (Denevan, 2014; Dobyns, 2017) and changed where the surviving Indigenous people lived and how they used the forest (Dobyns, 1983; Urzedo & Chatterjee, 2022). Although largely unstudied, the higher intensity of disturbances (e.g., mechanized deforestation) during the post-colonial period, which happened after previous disturbances during the pre-contact period, may have resulted in stronger or compounded ecological legacies that have yet to be examined (McMichael, 2021).

Pre-contact and post-colonial human settlements and their ecological consequences have been poorly studied in the relatively isolated rainforests in the Guiana Shield (Bodin et al., 2020; Hammond, 2005; Odonne et al., 2019). During the pre-contact period in Suriname, the Koriabo culture inhabited inland forests, but overall pre-contact settlements are understudied and hypothesized to be small (Versteeg, 2003). After European colonization, Maroons, descendants of enslaved Africans, escaped from coastal plantations and settled in the Surinamese rainforests where they still live today (Price, 1983). Maroons practice shifting cultivation and depend on hunting for their protein sources (Fleskens & Jorritsma, 2010; Price, 1991; van Andel et al., 2016; Appendix S1). Maroons grow a variety of Old-World crops that were brought to Suriname's forested interior during the post-colonial period, including bananas (Musaceae) and rice (Oryzoideae) (van Andel et al., 2016).

Here we assess the extent of ecological legacies on Surinamese forests through charcoal and phytolith analysis of 15 soil cores radiating up to 10 km from Beng Tapu, a recently excavated archaeological site that dates to the mid-18th century post-colonial period (Figure 1). We researched whether (1) past human activities occurred during the pre-contact and post-colonial period, (2) land use was most intensive within 1 km of the archaeological site, (3) evidence of fire and altered plant abundances occurred within a 10 km radius of the site, and if (4) human activities that occurred during the post-colonial period left stronger or more persistent legacies on modern forests compared to pre-contact activities. We expect that evidence of fire (charcoal), cultivation (maize, banana), forest opening, and plant enrichment practices occurred during both the pre-contact and post-colonial periods, but that the strongest ecological legacies were a result of forest modifications during the post-colonial period.

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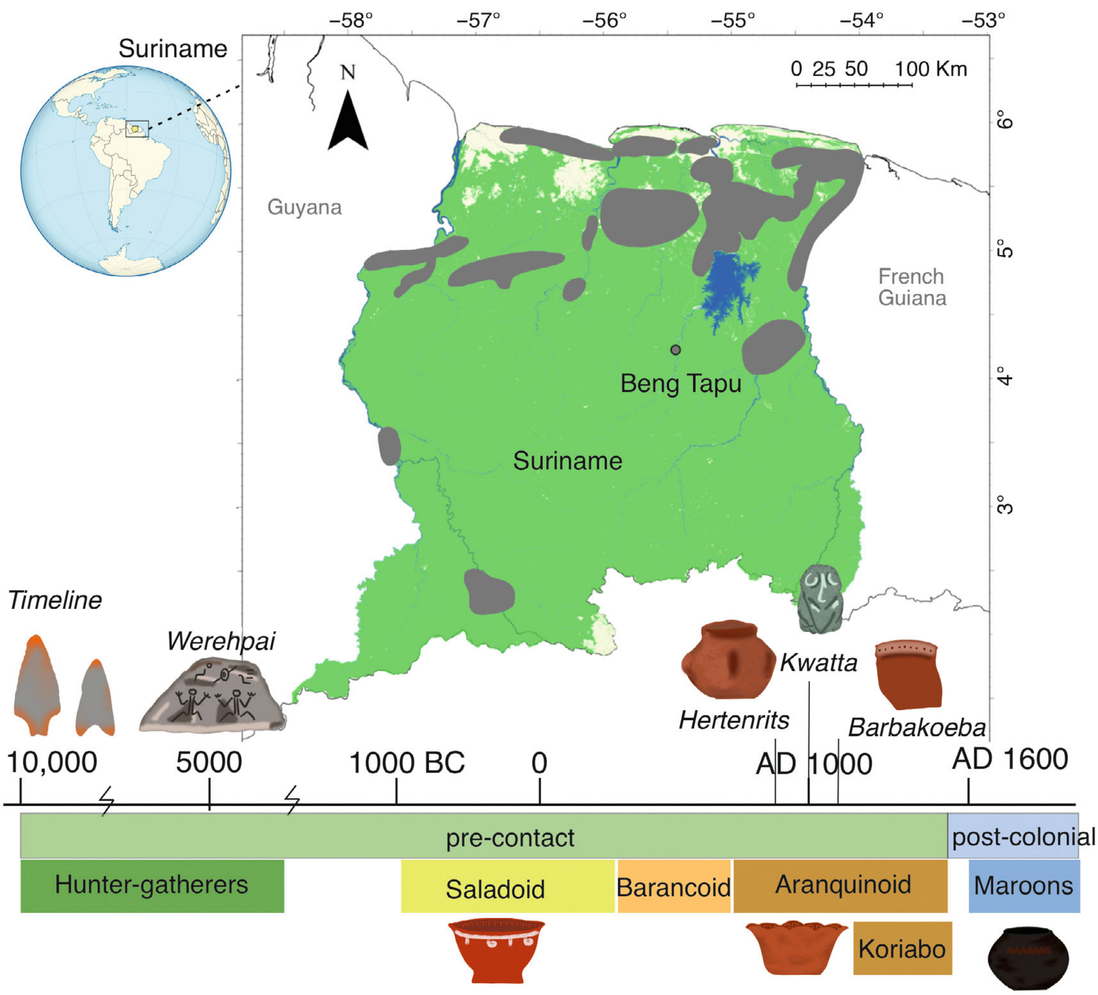

FIGURE 1 Map of Suriname, a timeline of pre-contact and post-colonial human history prior to AD 1700, and our study area near archaeological site "Beng Tapu." Gray polygons indicate areas that contain pre-contact archaeological sites (specific sites are in Versteeg, 2003). Illustrations were made by N. H. Witteveen.

METHODS

Study sites and sampling method

The Beng Tapu archaeological site (04°13′878″ N, 055°26′597″ W) is located in the Sipaliwini district of Suriname (Figure 1; Appendix S1: Figure S1). The climate of Beng Tapu is tropical with a mean annual temperature of 27°C and mean annual precipitation of 2200 mm (De Graaf et al., 1999) that falls during two wet seasons (April/May to August and December to January). Local vegetation consists of mesophytic forest (SBB, 2017), with shifting cultivation being practiced by Saamaka Maroons within 7–10 km of the Suriname River (National Land Monitoring System of Suriname, 2016).

In October 2021 we established two 10 km transects radiating from Beng Tapu. Soil cores were collected at 250, 500 m, and 1, 2, 4, 8, and 10 km away from the Beng Tapu site (Appendix S1: Table S1). Sampling sites were reached using a forest trail (F1–F8, A1, Pf1-2), a road (C), or a new (cut) trail (F1, F8), and soil cores were collected at least 20 m away from the path. Soil cores were collected in a cultivation area, abandoned sites, secondary forests, and forests outside the range of modern cultivation practices (Appendix S1: Figure S1). We dug a total of 15 soil cores and, for each core, samples were collected at 10-cm intervals up to an 80-cm depth (or when bedrock or groundwater levels were reached). We also collected a soil surface sample at the location of each soil core. All surface samples ($N = 15$) and soil core samples ($N = 102$) from the 15 soil cores were analyzed for phytoliths and charcoal. Soil cores were orange, clayey, and contained little organic matter (except for the brown surface samples). Basal samples often contained small red rocks (or sandstones). Soil cores Pf1 and Pf2 had a different color (white-gray) and texture (coarse) and contained more sand.

Laboratory analyses

Phytoliths were prepared from 117 samples from 15 soil cores using standard laboratory procedures

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(Piperno, 2006; Witteveen et al., 2023). For each sample, 1 cm^3 of unsieved soil was subsampled (the sand fraction was not fractionated, concentrated, and studied). For each subsample, 56,000 microspheres were added. Samples were then submerged in 33% H_2O_2, boiled on a hot plate, and then treated with $K_2MnO_4^-$ and 10% HCl to remove organic matter and carbonates. Next, samples were decanted until clear to remove clay material. Last, phytoliths were extracted from the sediment by heavy liquid flotation, using Bromoform with a specific gravity of 2.30, and mounted on slides using Permount. Phytoliths were counted until a minimum of 200 arboreal and a total of 400 phytoliths were reached, using a Zeiss Axioscope microscope with immersion oil at ×1000 magnification. Phytolith identification was based on the latest literature and nomenclature (Chen & Smith, 2013; Collura & Neumann, 2017; Huisman et al., 2018; Iriarte, 2003; Piperno, 1985; Piperno & McMichael, 2020, 2023; Witteveen et al., 2022). Phytolith morphotypes were put in 20 groups according to morphotype or taxonomic group (Table 1; Appendix S1: Table S2), making use of modern species occurrence data (Henderson et al., 2019; Witteveen et al., 2023). Phytolith results were plotted in relative abundance (in percentage) or presence (dots) using the *tidypaleo* and *tidyverse* packages in RStudio (Dunnington et al., 2022; Wickham & Wickham, 2017).

We identified charcoal and calculated charcoal volumes from all soil samples ($N = 117$, from 15 soil cores) to identify charcoal and calculate charcoal volume. A handful of soil was used for each sample, recording the dry weight (ca. 20–70 mg) and the initial volume of the soil. Samples were soaked in 200 mL of surfactant (Alconox) for 48 h and heated to 150°C for 40 min. Next, samples were rinsed through a 500-μm sieve, and the remaining contents were examined for charcoal using an Axiophot stereomicroscope. All charcoal fragments were photographed using a Fuji camera and the surface area was collected using ImageJ software (Abràmoff et al., 2004). Charcoal volume (in cubic millimeters per cubic centimeter) was calculated using the sum of the surface area (in square millimeters) of each fragment of charcoal and the starting volume of each sample (Weng, 2005).

TABLE 1 Phytolith morphotypes counted in this study, the corresponding plant taxa or group and if the morphotype indicates a specific vegetation type or disturbance.

Phytolith morphotype	Plant type or taxa	Indicates? (in rainforest setting)
rugose SPHEROID	Arboreal	Forested vegetation
ornate SPHEROID	Arboreal	Forested vegetation
SPH_ECH (Morcote-Ríos et al., 2016)	Palms	Forests, secondary forests, disturbed areas
Conical	Palms	Forests, secondary forests, disturbed areas
wavy-top RONDEL (Iriarte, 2003)	Maize	Cultivation, farming
CROSS 1 (>21 μm)	Maize	Cultivation, farming
T2 trough (Chen & Smith, 2013)	Banana	Cultivation, farming (in the post-colonial period)
CROSS 1, CROSS, BILOBATE, RONDEL, Other grass, Panicoideae, Bambusoideae, Chloridoideae, Pharoideae, Pooideae, Oryzoideae	Poaceae grasses	Openness, deforestation, or understory (Bambusoideae)
Perforated plates	Asteraceae	Openness
Polygonal shape, papillate shape	Cyperaceae	Openness, lakeshore vegetation
Wavy trapezoid	Pooideae	Cultivation, farming (Witteveen et al., 2023)
Seed phytoliths (Eichhorn et al., 2010)	Commelinaceae	
Scooped bilobate	Oryzoideae	
Druses (Chen & Smith, 2013)	Cannaceae, Costaceae, Marantaceae, Strelitziaceae	Openness, canopy gaps
Knobby (Chen & Smith, 2013)	Heliconiaceae, Marantaceae	
T1 trough (Chen & Smith, 2013)	*Heliconia*	

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Data analysis

To assess if past human activities occurred during the pre-contact and post-colonial periods, we obtained ages from charcoal (from past fire activities). In total, 12 charcoal fragments were large enough for ^{14}C AMS radiocarbon dating, and were sent to DirectAMS (Seattle, Washington, USA). Among the soil cores, C and BT1 presented numerous fragments suitable for radiocarbon dating and, in these cases, we opted to date the uppermost samples to obtain the age of the most recent fire event. Raw ^{14}C dates were calibrated using the "calibrate" function of the *rcarbon* package in R, with the IntCal20 calibration curve (Reimer et al., 2020). The ages of charcoal whose radiocarbon date came back as "modern" were calculated using the percentage of modern carbon and the "pMC.age" function of the *IntCal* package (Blaauw, 2010).

To research if vegetation changes occurred across space or time, detrended correspondence analysis (DCA) was used to assess the (dis)similarity between phytolith assemblages from each depth interval and each soil core. Rare palm genera and grass subfamilies were merged to create 13 phytolith groups (rugose SPHEROID, ornate SPHEROID, nodular SPHEROID, Other Woody, Conical, SPH_ECH, Poaceae, Heliconia, Zingiberales, Cyperaceae, Druses, Banana, and CROSS 1) that were used in a DCA, which was performed using the "decorana" function from the *vegan* package in RStudio (Dixon, 2003; Oksanen et al., 2013). Also, we researched how plant abundances changed across soil cores collected in the 10-km transects by analyzing the trend of change (percent in surface sample – percent in basal sample; TOC) and magnitude of change (maximum percent – minimum percent; MOC) for the five most common phytolith groups (rugose and ornate SPHEROID, SPH_ECH, Conical, Poaceae). Basal samples were between 50 and 80 cm in depth. The trend of change calculations indicated whether arboreal, palm, or grass phytoliths increased or decreased across the depth of each soil core, which we interpret as vegetation changes through time. The magnitude of change calculations indicated which soil cores contained the largest increase or decrease for a given phytolith type.

To assess if land use was most intensive within 1 km of the archaeological site, the evidence of past fire (charcoal volume), deforestation (percentages of open or disturbance phytoliths—see Table 1), and cultivation practices (the presence of maize or banana phytoliths) were compared across each transect. Past changes in biomass and openness were estimated by using the total arboreal phytoliths (in percentage) and openness values for each sample and comparing our values to calibration datasets based on modern phytolith–environment relationships (Witteveen et al., 2023). The openness index is the ratio of arboreal trees to grass phytoliths (Alexandré et al., 1997). Openness values <10 and low arboreal abundances (<50%) were found in forest openings >0.5 ha (Witteveen et al., 2023). We extracted modern aboveground biomass (ABG) values (Avitabile et al., 2016) for each soil core using the extract function of the package *raster* (Hijmans et al., 2013), and compared across biomass values to the history of past human activities at each site.

RESULTS

Charcoal was present in 84 of the 117 samples, and in all 15 soil cores, however 52 samples contained minute amounts (<1 mm^3/cm^3; Figure 2). Radiocarbon-dated charcoal fragments ($N = 12$) from soil cores indicated that fires occurred between 96 BC and modern times (Figure 2; Appendix S1: Table S3). Seven dated charcoal fragments were pre-contact in age (96 BC to AD 1381), and the other five were post-colonial in age (AD 1661 to modern). Seven dated fragments were obtained from within 1 km of the Beng Tapu archaeological site, where large charcoal volumes >10 mm^3/cm^3 were recovered. In general, charcoal volumes were higher in the top 20 cm of a soil core across all sites (Figure 2).

We identified 61 phytolith morphotypes in the 117 samples, including arboreal phytoliths (from Chrysobalanaceae, Malvaceae, and Moraceae), Poaceae phytoliths, and palm phytoliths from *Attalea*, *Astrocaryum*, *Euterpe*, *Geonoma*, *Mauritia*, and *Oenocarpus* (Appendix S1: Table S2). Rare phytoliths (<1%) included Pharoideae, Commelinaceae, Asteraceae, Cyperaceae, and Zingiberales. Maize phytoliths occurred within 1 km of the Beng Tapu site at soil cores BT2 and Pf1, in basal and surface samples (Figure 2). Size measurements showed CROSS 1 phytoliths, indicative of maize and Panicoideae (Table 1), were larger within 1 km of the archaeological site (Appendix S1: Table S4). Banana phytoliths occurred within 5 km of the site at soil cores F5, C, A1, BT1, and A2. Commelinaceae was identified at soil core Pf1, Pooideae at A1 and Oryzoideae at C, A1, and BT1. Druses and Knobby phytoliths were present in all soil cores, *Heliconia* occurred in all cores except soil core F2. Asteraceae was present in all soil cores except F1 and Pf2, and Cyperaceae was present in all soil cores except F2 and F3. Although phytoliths from Knobby, *Heliconia*, and Asteraceae were present across the transect, these morphotypes were identified in most samples from soil cores within 1 km of Beng Tapu, while occurring only once or twice in a soil core >1 km away from Beng Tapu (Figure 2).

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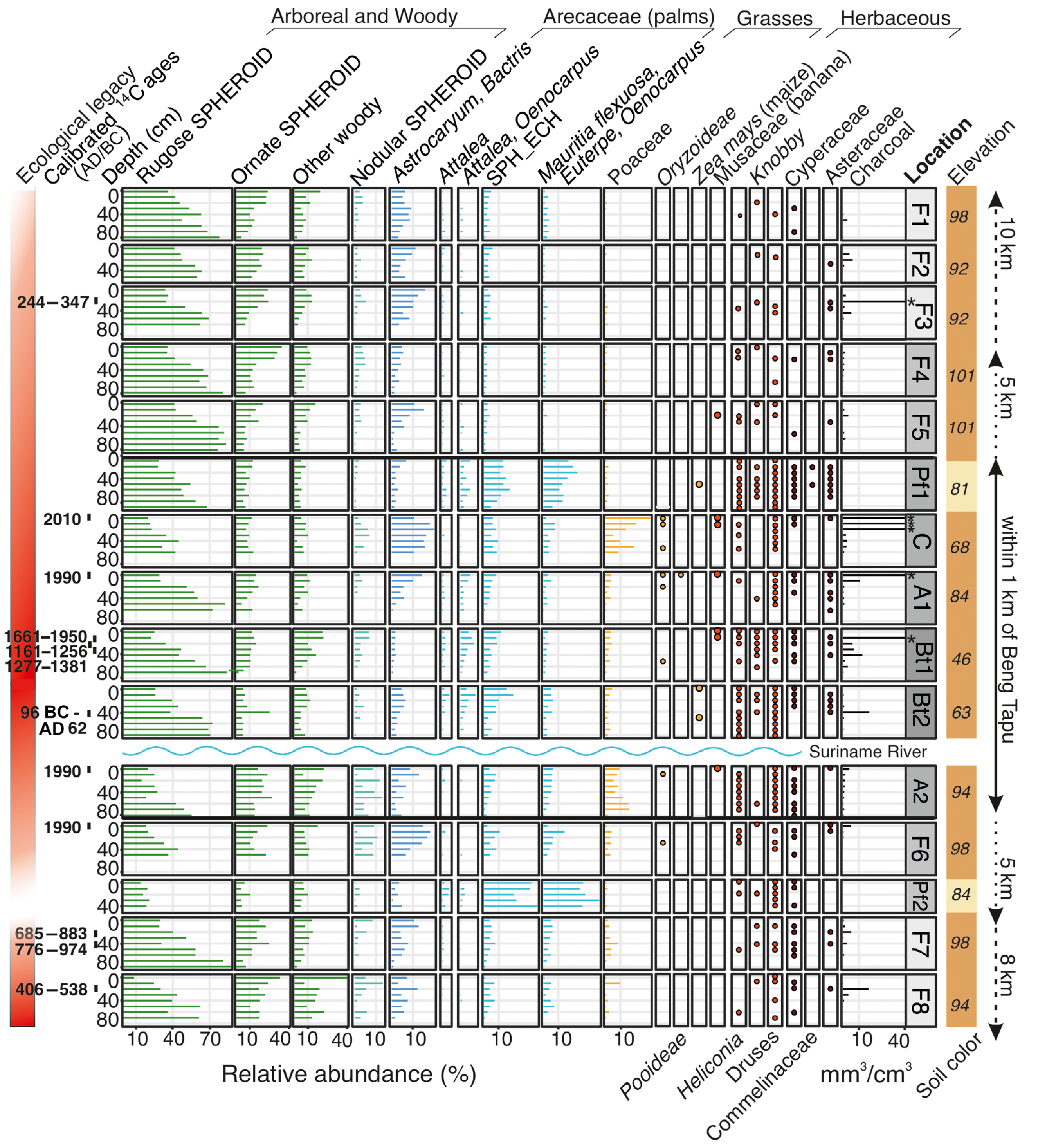

FIGURE 2 The relative abundances of phytolith types for each location and depth interval. The *y*-axis shows depth of the soil cores in 10 -cm intervals, the *x*-axis shows the phytolith relative abundance (in percentage), phytolith presence (dots) and charcoal volume (in cubic millimeters per cubic centimeter). Ecological legacies (in red), ^{14}C calibrated ages (in AD/BC), elevation (in meters above sea level), soil color, location, and distance to the archaeological site Beng Tapu are also shown. Orange dots (Pooideae, Oryzoideae) are grasses, red dots (Marantaceae, Musaceae, Knobby, *Heliconia* and druses) are Zingiberales. SPH_ECH palms are produced by *Attalea*, *Euterpe*, *Oenocarpus*, *Hyospathe elegans*, and *Cocos nucifera*.

Across the transect, altered arboreal and palm phytolith abundances were seen from basal to top samples. First, *Attalea* and *Oenocarpus* (specific) palm phytoliths increased at the archaeological site. Second, SPH_ECH phytoliths produced by *Euterpe*, *Oenocarpus*, *Attalea*, *Hyospathe elegans* or *Cocos nucifera* increased within

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1 km of the archaeological site. Third, phytoliths from *Astryocaryum* or *Bactris* increased within 8 km of the archaeological site, in soil cores where charcoal occurred. In contrast, however, palm phytoliths did not increase at Pf2 but remained high at every depth. Finally, ornate SPHEROID increased between 5 and 10 km of Beng Tapu and rugose SPHEROID decreased in all soil cores except Pf2 (Figure 2). Acanthaceae, Burseraceae, Lecythidaceae, Violaceae, and Vochysiaceae produce ornate SPHEROID and Chrysobalanaceae produces rugose SPHEROID in abundance (Piperno & McMichael, 2020), all families common in Surinamese rainforests (Funk et al., 2007).

Within 1 km of Beng Tapu, arboreal abundances were <50% and openness values <10 (Figure 3). The combination of low arboreal abundances (<50%) and openness values <10 also occurred at F7 (10–20 cm and 30–40 cm) and F8 (0–10 cm), which are located 6 and 8 km from Beng Tapu. Furthermore, elevated grass abundances (ca. 8%–10%) at F7 and F8 were paired with charcoal remains. High charcoal abundances >10 mm^3/cm^3 also occurred at F3 (6 km from Beng Tapu), but evidence of forest opening was absent (Figure 2). For other soil cores between 2 and 10 km of the archaeological site, openness values decreased from basal to top samples but ranged between 10 and 664 (values >10 indicate forested settings).

DCA results indicated that the major differences in vegetation variation occurred from the bottom toward the top of the soil cores, highlighting the importance of trends of change through time shaping modern vegetation (Figure 4a). Phytoliths from samples within the upper 10 cm of soils were most similar to the phytoliths collected from modern cultivation sites, and phytoliths from basal (50–80 cm) parts were closest to rugose SPHEROID produced by arboreal and woody taxa. Pf2 is the only soil core that does not show a change through depth (Figure 4a).

The largest magnitude of vegetation change (Figure 4b) occurred in soil cores BT1, A1, F7, and F8, seen by the largest decrease in rugose SPHEROID that was paired with an increase in palms and ornate SPHEROID. While soil cores BT1 and A1 were within 1 km of the archaeological site Beng Tapu, sites F7 and F8 were located at a 6–8 km distance, indicating that the largest magnitude of vegetation change was not related to the distance from the archaeological site.

DISCUSSION

Radiocarbon-dated charcoal fragments ($N = 12$) of soil cores confirmed our hypothesis that the area was used in the pre-contact and post-colonial period from 96 BC to recent times. Charcoal from pre-contact burning events that occurred centuries apart suggests there were multiple occupations within the region before European colonization, aligning with patterns seen in other Amazonian studies (Arroyo-Kalin, 2010; Arroyo-Kalin & Riris, 2021; Lins et al., 2015; Maezumi et al., 2018; Versteeg, 2003; White, 2010). Markedly, there have been no investigated pre-contact settlements in the vicinity of the study region, limiting our interpretation of this period. While the nearest archaeological site (Kumako, 40 km northwest) also reflects pre-contact and post-colonial occupation (White, 2010), the scarcity of archaeological studies in the forested interior of Suriname is noteworthy (Figure 1). Radiocarbon dating from excavations at Beng Tapu revealed that colonial metal, soft paste earthenware potsherds, and hard-paste ceramics recovered in a charcoal lens confirmed that Beng Tapu is the traditional territory of the Saamaka Maroons who settled in the late 17th century and remain so to this day (Appendix S1: Figure S2). Our analyses from Beng Tapu demonstrate the need for a broader discussion on the cultural overlap and exchange of pre-contact Indigenous and post-colonial tribal peoples. Our results highlight the complexity of past Indigenous and tribal land use. Especially in data-poor regions like Suriname, additional palaeoecological and archaeological research is needed for deeper insights into the cultural history and ecological heritage of Indigenous and tribal communities.

We hypothesized that land use was most intensive within 1 km of the Beng Tapu archaeological site and, correspondingly, maize phytoliths were identified only within 1 km of Beng Tapu. Maize was potentially grown during both the pre-contact and post-colonial periods, because it occurred in basal and top samples (Figure 2). Also, within 1 km of the site, charcoal volumes were highest and more phytoliths indicative of disturbances or forest opening were present, supporting our hypothesis that land use was most intensive within 1 km of Beng Tapu. In contrast, phytoliths associated with Maroon cultivation practices, including banana, Pooideae, Chloridoideae, Commelinaceae and Oryzoideae (Witteveen et al., 2023), were found up to 5 km from Beng Tapu. Because banana is not native to South America, its phytoliths suggest post-colonial cultivation practices (Castilla-Beltrán et al., 2018). Thus, our data suggest that cultivation was practiced up to 5 km of the archaeological site during the post-colonial period.

Within 1 km of the Beng Tapu archaeological site, modern above-ground biomass (AGB) estimates (Avitabile et al., 2016) were the lowest (<200 Mg/ha), suggesting persistent ecological legacies have occurred from pre-contact and post-colonial fire and cultivation practices (Figure 3). Within 5 km of Beng Tapu, where

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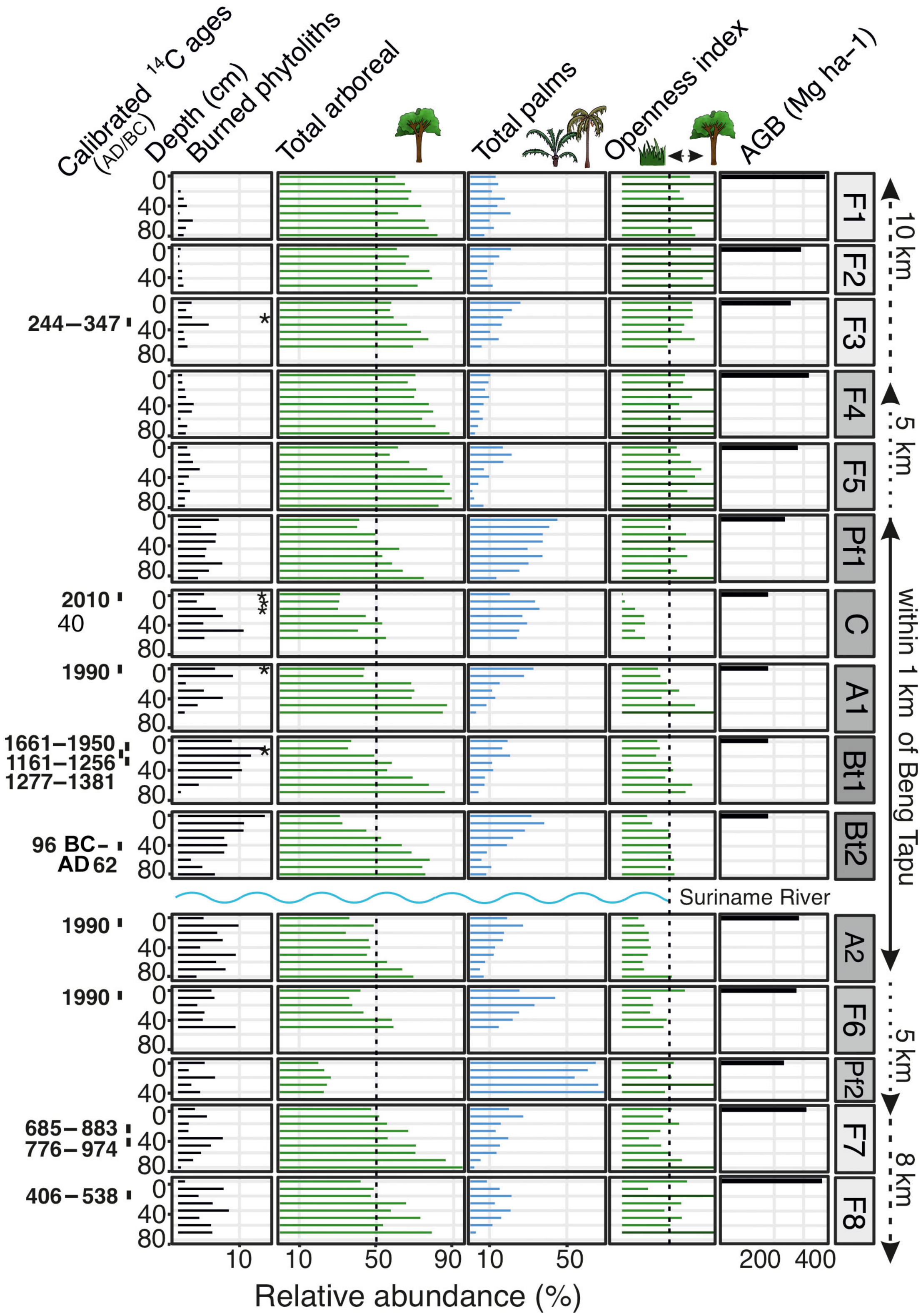

FIGURE 3 Diagram showing ^{14}C calibrated ages (in AD/BC), burned phytoliths (black), total arboreal (green) and total palm (blue) phytoliths in abundance (in percentage), log-transformed openness index values (green) and aboveground biomass (black) estimates in megagrams per hectare (Avitabile et al., 2016). Stars indicate samples with high charcoal volumes >10 mm^3/cm^3. Dark green bars indicate samples with no grass silica short cell phytoliths, and values below dashed lines suggest forest opening (Witteveen et al., 2023). The *y*-axis shows depth in 10-cm intervals for each location, the distance to the archaeological site Beng Tapu and Suriname River are indicated. Illustrations were made by N. H. Witteveen.

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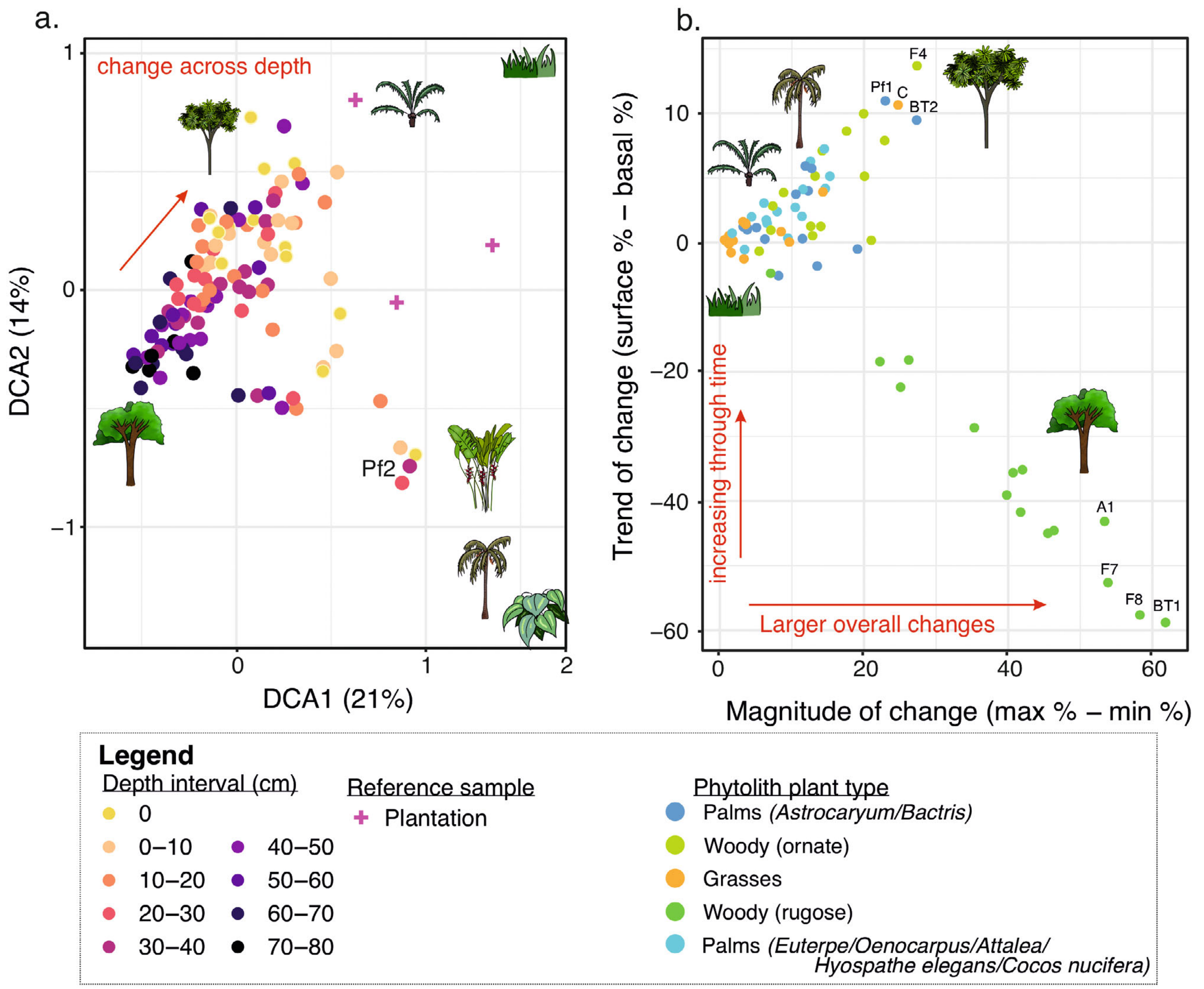

FIGURE 4 (a) Detrended correspondence analysis (DCA) of phytolith percentage data from all the sampled sites, colored by depth. Red arrows show the trend or magnitude of change across depth/time. (b) Trend of change (y-axis) using surface to basal samples and magnitude of change (x-axis) using maximum to minimum values of the abundances (in percentage) of palms (blue), woody (green) and grass (orange) phytoliths. Illustrations were made by N. H. Witteveen.

post-colonial cultivation practices have occurred, AGB estimates ranged between 284 and 404 Mg/ha and overlapped with AGB estimates >5 km away (274–433 Mg/ha), all values that fell within the range of biomass estimates for Amazonian forests (Brown & Lugo, 1992; de Castilho et al., 2006; Nascimento & Laurance, 2002). Collectively, our results suggest that evidence of both pre-contact and post-colonial cultivation practices within 1 km of Beng Tapu left persistent ecological legacies on modern biomass, but the post-colonial legacies that extended up to 5 km of the site did not.

Burning events and forest openings were not restricted to areas close to Beng Tapu as hypothesized, but were also found at 6 and 8 km distance from the site (Figure 2). This is likely because the charcoal at F3, F7, and F8 were dated to the pre-contact period and Beng Tapu is a mid-18th century archaeological site. The F7 and F8 sites may be close to a yet undiscovered pre-contact occupation site across the Suriname River. It is hypothesized that pre-historic occupation sites were not adjacent to, but located at least 8–10 km apart from, each other, because this “buffer” prevented competition for resources (Denevan, 1996). The high charcoal volume at F3, in the absence of signs of deforestation, may suggest this was a single fire event (AD 244–347) with a nonpersistent impact on the vegetation. The largest magnitude of vegetation change (at soil cores BT1, A1, F7, and F8) was also not related to the distance near the Beng Tapu site, but these soil cores all contained large volumes of charcoal (Figure 2). These data highlight the

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significant impact that fire can have on vegetation turnover in tropical forests (Barlow et al., 2003; Barlow & Peres, 2008).

Palm abundances increased across all soil cores in the transects, from basal to top samples, as indicated by the TOC analysis. The increases in *Attalea* and *Oenocarpus* (specific) phytoliths could be a direct enrichment due to culinary uses. Several burned seeds of *Attalea maripa* were found during the archaeological excavation, which Saamaka Maroons use to produce oil (van Andel & Ruysschaert, 2014). Second, increases in SPH_ECH phytoliths within 1 km of the archaeological site could be related to increases in *Attalea* and *Oenocarpus*, because these palms are adapted to open conditions and fire (Henderson et al., 2019), whereas many Amazonian tree species are not adapted to fire (Uhl & Kauffman, 1990). Finally, it is hypothesized that people influenced the occurrence of *Astrocaryum vulgare* and *Astrocaryum aculeatum* in Suriname and *Astrocaryum sciophillum* in French Guiana (Boer, 1965; Odonne et al., 2019), as these species have been reported to grow in disturbed forests or near archaeological sites. Our results support this hypothesis and show that *Astrocaryum* palms increased in soil cores with past fire events and in the area where modern shifting cultivation occurs (Appendix S1: Figure S1). The different palm increases within 0, 1, and 8 km of the archaeological site might reflect direct enrichment (*Attalea*) versus indirect enrichment (*Astrocaryum*) because both genera include palms that are adapted to fire and open habitats (Henderson et al., 2019; Smith, 2014).

In contrast with the above-mentioned findings, however, no evidence of palm enrichment was detected at Pf2 (Figure 2). This location was dominated by *Euterpe oleraceae*, a hyperdominant species widely used to build houses and fences, as food and juice (van Andel & Ruysschaert, 2014), and was located near a vegetation marker for archaeological sites (a *Ceiba pentandra* tree). An explanation for the high abundance of *Euterpe oleraceae* may be local edaphic and hydrological conditions, as *Euterpe oleraceae* reportedly grows near creeks and in swampy areas (Johnston, 1998; Ter Steege et al., 2013; van Andel, 2000; van Andel & Ruysschaert, 2014). Interestingly, both palm-dominated forests (Pf1, Pf2) contained soils that appeared white and sandy instead of orange and clay, suggesting higher sand concentrations than other locations (Figure 2). In central Amazonia, palm densities are higher on sandy soils compared with clay-rich soils (de Castilho et al., 2006). Soil, hydrology, and topography are known important drivers of palm community composition (Eiserhardt et al., 2011; Svenning, 1999, 2001; Vormisto et al., 2004) and may also explain the locally high palm abundances at Pf1 and Pf2.

Changes in forest composition that occurred in the absence of major fire or forest opening events may be a part of natural forest dynamics or an indirect effect of hunting activities (Antunes et al., 2016; Peres et al., 2016; Peres & Lake, 2003; Peres & Nascimento, 2006; Shepard Jr et al., 2012). Many hardwood trees rely on game animals for seed dispersal (Aldana et al., 2017; Bello et al., 2015; Correa et al., 2023), and hunting causes a decline in various animal species that play a vital role in long-distance seed dispersal (Ouboter et al., 2021; Van Kuijk et al., 2022). It is also possible that post-colonial logging activities have depleted species in forests near archaeological sites (Levis et al., 2017; Odonne et al., 2019). Modern studies have shown that logging has impacted forest succession for decades (De Graaf et al., 1999; Dekker & De Graaf, 2003; Landburg et al., 2021). However, it remains to be tested if post-colonial hunting or logging activities can result in indirect legacies (Boomgaard, 1992).

Saamaka Maroons settled along the upper Suriname River region in the late 1600s. They practiced an intratribal settlement pattern along the riverbanks after peace treaties were signed in the 1760s (Jagdew, 2014). Based on preliminary analysis of artifact assemblages, oral historical testimonials and archival evidence, the archaeological site of Beng Tapu may have been settled by Saamaka Maroons (C. White, personal communication, May 25, 2023). The combination of banana phytoliths and charcoal remains was dated to AD 1661–1789 suggesting that shifting cultivation was practiced within 5 km of Beng Tapu by Saamaka Maroons (Figure 2; Appendix S1: Figure S3).

DCA results suggested that large vegetation changes have occurred in the past, especially in the upper 10 cm of soil cores (Figure 4). Although not all samples were dated, five of these contained banana phytoliths, indicating that these changes occurred in the post-colonial rather than the pre-contact period. Additionally, charcoal volumes were generally higher in the top 20 cm of a soil core, which could suggest an increased fire intensity in the post-colonial period (Figure 2). Previous studies have shown that the upper 20 cm of soil cores may encompass pre-contact and post-colonial periods (Heijink et al., 2023; McMichael et al., 2022; Piperno et al., 2021). Because Beng Tapu represents a mid-18th century archaeological site, increased charcoal volumes in the upper layers are likely attributed to the post-colonial period. Overall, these results suggested that the impact of human activities from the post-colonial period left stronger or more persistent legacies on modern forests compared with the pre-contact activities. Modern deforestation and agricultural activities make it difficult to determine the impact of past human activities at soil

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cores C, A1, and A2. Phytoliths have a downward mobility under natural conditions (Fishkis et al., 2010). Because land tillage near Beng Tapu is done manually, disturbances >50 cm depth are not expected but soil core C may have been exposed to soil erosion or overturning from recent slash-and-burn activities (Fleskens & Jorritsma, 2010).

Our findings suggested that ecological legacies from past human activities are more common near river margins, which is in agreement with previous work from the western and central areas of Amazonia (Bush et al., 2015; Levis et al., 2017; McMichael et al., 2012; Piperno et al., 2021; Zuquim et al., 2023). Beng Tapu is situated within 1 km of the Suriname River, making it easily accessible by boat and abundant in terrestrial and aquatic resources. Nowadays, Saamaka Maroons hunt animals like collared peccaries (*Tayassu tajacu*), which migrate seasonally in large herds across the rivers. Similar riverine and lake areas in Amazonia have been occupied multiple times in the late Holocene (Åkesson et al., 2021, 2023; Maezumi et al., 2018), and pre-historic occupation sites are more probable within 15 km of a river floodplain (Bush et al., 2015).

The findings of the current study, however, do not support spatially extensive and persistent ecological legacies in Amazonia (Franco-Moraes et al., 2019; Levis et al., 2017; Prümers et al., 2022), as our results showed that two millennia of past human activities had left a diminishing ecological legacy within several kilometers of the occupation site. This discrepancy may be explained by differences in the density of past populations and settlements, and with that their activities, transient nature and impact on the forests (Piperno et al., 2017; Prümers et al., 2022). Several sites in northwestern Amazonia have also shown no or a small (<1 km) impact due to past human activities (Heijink et al., 2020; McMichael et al., 2012; Piperno et al., 2021), further supporting heterogenous ecological legacies in Amazonia. Therefore, it is important not to extrapolate data across Amazonia, but to expand archaeological and palaeoecological research in data-scarce regions to understand these forests in their historical context.

We suggest that the timing (time since land use), intensity, and frequency of past disturbances all determine modern vegetation patterns at or near (former) occupation sites. Therefore, the cumulative effects of human activities during the pre-contact and post-colonial periods could leave ecological legacies on modern Amazonian forests (McMichael, 2021). Future studies should focus on the type and timing of disturbances that have resulted in ecological legacies, to understand if and how Amazonian forests recover from human disturbances.

Understanding the ecological consequences of past human activities leads to insight into (long-term) forest recovery. Our results highlighted the significance of disturbance frequency, type, and intensity for long-term forest recovery, and showed localized, but sometimes persistent, ecological legacies after two millennia of land use. Changes in species composition and associated plant traits ultimately impact ecosystem processes and functioning (Bruelheide et al., 2018; Fortunel et al., 2016), and its resilience to withstand current anthropogenic or climatic pressures. The challenge now is to assess forest resilience in the face of various legacies, to inform conservation strategies (McMichael et al., 2023). Finally, integrating traditional ecological knowledge into research and conservation efforts can enhance our understanding of historical legacies and contribute to sustainable management practices (Best et al., 2021; Peterson & Heemskerk, 2001).

AUTHOR CONTRIBUTIONS

Fieldwork: CW, SS, NHW. *Laboratory analysis*: NHW, BAS, AP, RB, FB, RC. *Data analysis*: NHW. *Writing—original draft*: NHW. *Writing—review and editing*: CW, CNHM, WDG, DP. *Conceptualization*: NHW, CNHM, WDG, CW.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Witteveen et al., 2024) are available in figshare at https://doi.org/10.6084/m9.figshare.25060217.

ORCID

Nina H. Witteveen https://orcid.org/0000-0003-0214-4238
William D. Gosling https://orcid.org/0000-0001-9903-8401
Dolores R. Piperno https://orcid.org/0000-0002-0584-3133
Crystal N. H. McMichael https://orcid.org/0000-0002-1064-1499

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